MORPHOLOGY AND SYSTEMATICS OF THE NORTHERN DVINA CYNODONTS (REPTILIA, THERAPSIDA; UPPER PERMIAN)

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ABSTRACT

The materials on the North Dvina cynodonts, *Dvinia prima* and *"Permocynodon sushkini"*, are redescribed. These cynodonts have a complete secondary palate, an interpterygoid vacuity of the therocephalian type, a medioventral contact between the basiptery-goid processes, and an additional mandibular articulation between the surangular and quadratojugal. In addition, I have found an impression of the external auditory meatus, which has a structure of the tritylodont type but runs to the region of the external quadrate condyle and is closely connected with the grooves for the veins in the occipital part of the skull. The problem of the position of the tympanum in theriodonts is discussed, and the opinion about the attachment of the tympanum to the medial quadrate condyle is criticized. Another very unusual feature is the structure of the lower "molars" of *Dvinia,* which are described for the first time in the present article; these "molars" have up to 22 additional cusps on the crown and differ sharply both from the upper "molars" of the same animal and, in general, from the "molars" of all previously known theriodonts. *Dvinia's* "molars", which are transversely widened, did not occlude; the lower "molars" lay interior to the upper and pressed the food against the secondary palate.

It is shown that three Northern Dvina specimens that were described as two separate species actually belong to the same species, *Dvinia prima*. The morphological peculiarities of this Northern Dvina cynodont justify its being set apart in a separate family Dviniidae related to the Procynosuchidae — the extremely primitive cynodonts of South Africa.

Contents

INTRODUCTION

The Northern Dvina cynodonts, *Dvinia prima* Amalitzky, 1922, and *"Permocynodon sushkini"* Woodward, 1932, were until very recently the only known representatives of this group of theriodonts from the U.S.S.R. Their anatomy was described primarily in publications by Y. D. Konzhukova (1946a, 1949). A number of aspects of the structure of *"Permocynodon"* had been noted earlier by P. P. Sushkin (1927, 1929), but *Dvinia* was known only from a preliminary description by V. P. Amalitzky (1922). Finally, the basipterygoid articulation, the labial portion of the skull, the mandibular articulation and some features of the venous circulation in the head of *"Permocynodon"* were described by the present author (Tatarinov, 1966a, 1966b, 1966c, 1967). In spite of all these publications, however, many aspects of the morphology of the Northern Dvina cynodonts have remained obscure. Among the things still to be learned were the systematic position of the Northern Dvina forms among the cynodonts, as well as the relationship of the two Northern Dvina genera to each other.

Amalitzky (1922) described only the dentition of *Dvinia*. He indicated that the upper postcanine teeth of *Dvinia* were divided into comparatively simple "premolars" and "molars" located just behind these; in addition, Amalitzky correctly described the arrangement of the cusps on the upper postcanines. Sushkin (1929) provided a very concise, and for the most part quite accurate, description of the skull of *"Permocynodon."* He not only noted the peculiar proportions of the cranium of *Permocynodon* but also described many important features of this form, especially the presence of an interpterygoid vacuity and the double nature of the mandibular articulation. With a few exceptions, Sushkin did not describe the position of the sutures between the various bones. Even before the publication of his description of *"Permocynodon,"* Sushkin (1927) noted certain aspects of the structure of the otic area of the skull in a special study of the comparative anatomy of the visceral skeleton of the lower tetrapods. He called particular attention to the contact between the stapes and the paroccipital process and to the presence of a foramen stapediale.

Konzhukova (1949) was the first to describe the remains of the postcranial skeleton associated with *"Permocynodon."* Of greatest merit was her detailed description of the upper postcanine teeth

of *"Permocynodon."* In this regard Konzhukova's work was an essential contribution to our knowledge of the morphology of the Northern Dvina cynodonts. But the descriptions of the *"Permocynodon"* cranium published by Konzhukova (1946a, 1949) contained many inaccuracies and was thus a step backward, as compared to Sushkin's work. Konzhukova, for example, failed to note the interpterygoid vacuity pointed out by Sushkin, the ossification of the anterior part of the brain case (the "orbitosphenoids", as Sushkin called it), the presence of a coronoid and a foramen stapediale, and other features. The mandibular articulation, according to Konzhukova, was not double, as Sushkin had correctly noted, but of the common single type. Konzhukova's indications of the sutures between the various bones of the skull are partly incorrect; study of the original specimen has shown that sutures in the area of the occipital condyle were drawn before the bones were completely cleaned of matrix rock. Konzhukova also repeated some of Sushkin's individual erroneous statements, for example, mistaking the fracture in the middle part of the nasal for the suture between the frontal and the nasal, and mistaking the vacuity at the anterior portion of the parietal crest for the parietal foramen.

The presence of defects and contradictions of this kind in the descriptions by previous authors, as well as the unclear systematic status of the Northern Dvina cynodonts, has made it desirable to publish the most detailed possible restudy of the cranial anatomy of *"Permocynodon"* and *Dvinia*. This has not only made it possible to correct many inaccuracies which had crept into previous descriptions of the Northern Dvina cynodonts, but has also revealed numerous previously unknown details of the anatomy of these animals. Of special interest are certain details of the structure of the brain case found by the present writer which provide an important contribution to our knowledge of the morphology of the cynodonts and, in some respects, indicate that these Upper Permian theriodonts are even closer than previously thought to the Mesozoic mammals.

MATERIALS AND METHODS

The present article is based on three specimens: the holotype *Dvinia prima* (the anterior half of the skull, Specimen PIN 2005/2465); the holotype *Permocynodon sushkini* (skull, Specimen

PIN 2005 2469); and a fragment of upper jawbone (Specimen PIN 2245 237) which Konzhukova (1949) assigned to *P. sushkini*. Restudy of the best preserved specimen, PIN 2005 2469, proved especially fruitful. With some specifically mentioned exceptions, the morphological description in this article is based on PIN 2005 2469.

Additional preparation of the specimens, which was done by the use of acids, proved to be exceedingly difficult, because of both the hardness and density of the matrix rock and the brittleness of the bones, which were shot through with numerous fractures. In some places the bones and especially the teeth suffered considerable damage during their preparation by previous investigators; for example, on the holotype *P. sushkini* the front end of the snout was obliterated, the lacrimal duct was broken open on the outside, the right stapes was broken off and the right side of the ventral surface of the otic capsule was destroyed. To reveal certain internal structures, the author was able to take advantage of some already existing fractures at various levels of the skull of PIN 2005 2469.

The drawings were made by the artist N. A. Yan'shinov.

SYSTEMATICS

THE RELATIONSHIP BETWEEN DVINIA AND "PERMOCYNODON"

The close similarity of the two Northern Dvina cynodonts was noted by Sushkin (1929). Yefremov (1940) suggested that *"Permocynodon"* was merely a young individual of *Dvinia* and dispensed with the name *Permocynodon* Sushkin, 1927. But Yefremov assumed that the two forms belonged to different species, and he mentioned neither similarities nor differences between *Dvinia* and *"Permocynodon"*. Konzhukova (1949) noted that *"Permocynodon,"* differs from *Dvinia* in 1) the greater development of the sagittal crest, 2) the more nearly circular cross sections of its canines, 3) the smaller number of its teeth, — 12 instead of 13, and 4) its smaller overall size. She also commented on the similarity of the two forms, but left open the question of whether they belonged to the same or different genera and species. These remarks evidently shook Yefremov's conviction that *Dvinia* and *"Permocynodon"* were synonymous, and in 1955 he reverted

to the different generic names for them (Yefremov and V'yushkov, 1955). Their generic independence was also assumed in *Osnovy Paleontologii* ("Fundamental Principles of Paleontology") (V'yushkov, 1964) and in some of the other important works (Huene, 1956; Romer, 1956; Lehman, 1961).

Analysis of the data and the actual materials, however, suggests quite strongly that both of the Northern Dvina cynodonts actually belonged to the same species. As for the four points of difference mentioned by Konzhukova (1949), the two "genera" actually differ only in overall size. The sagittal crest is not fully preserved in the holotype *Dvinia prima,* although the edges of the frontals which form its anterior base converge in this specimen exactly as they do in the *"sushkini"* holotype. This suggests that the sagittal crest extended for the same distance in both "genera". The canine teeth are clearly compressed laterally in both holotypes; the degree of this compression cannot be determined, however, because of their deformation. Finally, both *Dvinia* and *"Permocynodon"* may have had 13 postcanine teeth. To be sure, it is not impossible that the traces of the foremost "premolar", which has already been shed in the holotype *"Permocynodon sushkini",* have merely not been discovered in the holotype *Dvinia prima,* so that the latter thus actually had 14 postcanines. But the formation of additional teeth at the end of the tooth row as the animal grew older is common in the cynodonts (*Diademodon:* Fourie, 1963; *Thrinaxodon:* Hopson, 1964), so that this feature cannot serve as a basis for distinguishing between the two forms.

The point which finally convinced the present writer that both Northern Dvina cynodonts belong to the same species is the identical character of the differentiation of their postcanine teeth. In both forms the upper teeth (the lower jaw of the *Dvinia prima* holotype is unknown) are differentiated outwardly into "premolars" (I— VI) and "molars" (VII — XIII). The latter are widened transversely and have up to 10 additional cusps each, located chiefly along the anterior and posterior edges of the crown. This tooth structure is quite unusual for the Permian cynodonts, and the identical distribution of the additional cusps in all three known specimens of Northern Dvina cynodonts is sufficient proof that they are of the same species. Thus the generic name *Permocynodon* Sushkin, 1927, should be considered a junior synonym of

the name *Dvinia* Amalitzky, 1922; and the specific name *"Permo-cynodon" sushkini* Woodward, 1932 is a junior synonym of the name *Dvinia prima* Amalitzky, 1922.

THE SYSTEMATIC POSITION OF THE GENUS DVINIA AMALITZKY, 1922

None of the authors who has described or discussed the Northern Dvina cynodonts has dealt with the problem of their systematic position. They were first assigned by Woodward (1932) to the family Cynognathidae, into which this author placed all the "non-gomphodont" cynodonts. Watson and Romer (1956) assigned the Northern Dvina cynodonts to the family Procynosuchidae. Later on, however, Romer (1961) decided that according to its tooth structure, a sharp distinction should be drawn between *"Permocynodon"* and all the other cynodonts. Huene (1956) assigned *"Permocynodon"* to the Cynosuchidae (Galesauridae) and *Dvinia* to the Diademodontidae; apparently his justification for doing this was the similarity which Amalitzky (1922) noted between the postcanine teeth of *Dvinia* and of the gomphodonts. Finally, in *Osnovy Paleontologii* (V'yushkov, 1964) the Northern Dvina cynodonts were placed in the Galesauridae.

The results of the present writer's study offer a more reliable basis for the systematic classification of the Northern Dvina cynodonts *(Dvinia)*. The lower jaw structure with its well developed postdentary bones seems to leave no doubt that *Dvinia* belongs to the suborder Procynosuchia [for present purposes we use Brink's classification of the cynodonts (1963b,c)]. Within this group, however, *Dvinia,* which has an almost gomphodont differentiation of its teeth, occupies a completely isolated position. The presence of an interpterygoidal vacuity, rudimentary suborbital foramina and a rudimentary anterior canine tooth nevertheless justify the placing of *Dvinia* in the superfamily Procynosuchoidea, within which it must definitely be assigned to its own separate family:

Dviniidae Tatarinov, fam. nov.

DIAGNOSIS: Procynosuchoidea with a well developed secondary bony palate and a very long sagittal crest formed not only by the parietals but also by the posterior halves of the frontals. There is

no parietal foramen. The mandibular articulation is ventral to
and below the level of the occipital condyle. The surangular forms
a supplementary mandibular articulation with the quadratojugal.
The postcanine teeth are externally differentiated into conical
"premolars" and transversely widened "molars" with numerous
additional cusps. On the "molars" in the upper jaw the additional
cusps are ranged along the edges of the crown around the prin-
cipal cusp, and on the "molars" of the lower jaw principally
interior to the principal cusp. The family at present contains only
the genus and species *Dvinia prima* Amalitzky, 1922 (=
Permocynodon sushkini Woodward, 1932), from the Upper
Tatarian deposits of the Arkhangel'sk oblast (region).

MORPHOLOGY

THE ROOF OF THE SKULL

A characteristic feature of the Northern Dvina cynodonts is the
extraordinarily strong development of the sagittal (parietal) crest,
which extends along the entire posterior half of the skull and is
formed not only by the parietals, but also by the frontals, except
for the anterior half of the latter.

Both Sushkin (1929) and Konzhukova (1946a, 1949) mis-
takenly identified as the suture between the frontals and the nasals
what is actually a fracture in the middle part of the latter; this
fracture is present in both skulls. As a result, the nasals and the
frontals as shown by Konzhukova (1946a, Fig. 1; 1949, Figs. 1
and 14) have outlines which are highly unusual for the therio-
donts. Konzhukova's "frontals" are actually the posterior halves
of the nasals, and her "parietals" are combinations of the true
frontals and parietals. The "foramen parietale" mentioned by
Sushkin and illustrated by Konzhukova for PIN 2005 2469 is
actually merely a vacuity at the anterior end of the sagittal crest
bordered on the sides by the edges of the frontals rising up to form
the crest. This vacuity also occurs in PIN 2005/2465. A true
parietal foramen is lacking in *Dvinia,* probably because of the
intensive development of the sagittal crest. The lack of a parietal
foramen distinguishes *Dvinia* from all the primitive cynodonts
which Brink (1963b) combined into the infraorder Procynosuchia.

The prefrontals and lacrimals are much less strongly developed
than Konzhukova indicated (1946a, Fig. 1; 1949, Figs. 1 and

FIG. 1. *Dvinia prima* Amalitzky, ex PIN 2005/2469; dorsal view of the skull ($\times$ 1.8).

14). As in all cynodonts, but contrary to Konzhukova's descrip-
tion, the prefrontals do not adjoin the maxillae; they are bordered
at the front by processes of the nasals, which separate them from
the maxillae (Fig. 1).

Apertures between the maxillae and the septomaxillae, through
which, it was believed, the ends of the canines protruded when the
mouth was fully closed (Konzhukova, 1949), are actually lack-
ing. These "apertures" were actually holes formed by breakage
during the preparation of the very thin areas of the maxillae which
form the roof of the vacuities for the reception of the lower
canines. Sushkin also mistook this defect in preparation for a
natural aperture (Sushkin, 1929). There is a septomaxillary fora-
men (fsm) preserved only on the left side in the "sushkini"
holotype which is bordered by the maxilla, the septomaxilla and
the premaxilla and opens into the nasal cavity. This aperture was
not noticed previously, although it is shown in one of the illustra-
tions accompanying Sushkin's article (1929, Fig. 4).

A deep maxillary pit (fmx) is developed in the upper part of
the maxilla above the anterior (II-V) cheek teeth. A similar
pit is known to occur in many other theriodonts; in life this
probably contained a skin gland (Tatarinov, 1964). The nasomax-
illary pit, which is characteristic of many cynodonts, is absent in
the Northern Dvina forms. Posterior to the canines and in the
lower edge of the maxilla there is a pair of longitudinal grooves
which appear to have served as the attachment areas of the labial
muscles. In their location, the muscle grooves in *Dvinia* correspond
to the attachment areas of the muscles which elevate the upper lip
in the mammals — the M. levator labii superioris proprius and the
M. levator anguli oris, or M. caninus (Tatarinov, 1964).

The foramina of the infraorbital canal for the passage of the
vessels and nerves for the upper lip are few in number and
located in the area behind the canines. The anterior infraorbital
foramen opens at the level of postcanines II - III, and the poste-
rior foramen at the level of VI - IX. In addition to the two main
infraorbital foramina, both specimens of the Northern Dvina cyno-
dont have several additional and very small foramina. Two or three
of these emerge in front of and above the anterior infraorbital
foramen and one or two alongside the posterior infraorbital fora-
men. A small group of these apertures are connected with the

glandular pit in the maxilla. The muscle grooves show no connection with the vascular foramina for the blood vessels.

In contrast to the more primitive theriodonts of the *Moscho-whaitsia* type (Tatarinov, 1964), there are absolutely no impressions of the network of vessels and nerves for the upper lip in the maxilla and premaxilla in *Dvinia*. In this respect the Northern Dvina cynodonts resemble the mammals, in which the better developed vessels and nerves for the lip pass entirely through the soft tissues and leave no impressions on the bones. Along with direct indications of the development of the labial musculature, this circumstance suggests that the Northern Dvina cynodonts possessed at least rudimentary soft lips of the mammalian type (Tatarinov, 1967).

The anterior part of the nasal, as in *Thrinaxodon* (Estes, 1961), is penetrated by numerous apertures which apparently allowed passage of the branches of the medial ethmoid nerve (V_1) and their accompanying blood vessels; the principal branch of the lateral ethmoid nerve seems to have passed through the septomaxillary foramen (Tatarinov, 1964). On the ventral surface of the nasal are ridges for the nasoturbinal (in the *"sushkini"* skull it was possible to prepare only their anterior parts).

In the anterior wall of the orbit, between the processus ascendens of the palatine and the lacrimal, there is a fissure-like sphenopalatine foramen for the postnasal and the palatal vessels and nerves. This foramen was probably described by Bonaparte (1963a) in the traversodontid *Ischignathus* under the name "ethmoid." The foramen for the entrance of the lacrimal duct(dl) is double.

The muscle attachment process of the jugal, which is characteristic of the higher cynodonts (Watson, 1920), is lacking in the Northern Dvina forms.

The Palate

The Northern Dvina cynodonts are interesting for their combination of a well developed bony secondary palate with a typically "therocephalian" interpterygoid vacuity and miniature suborbital foramina between the ectopterygoids and the palatines (Fig. 2).

The palatal processes of the maxillaries and the palatines contact one another without forming a denticulated suture. The poste-
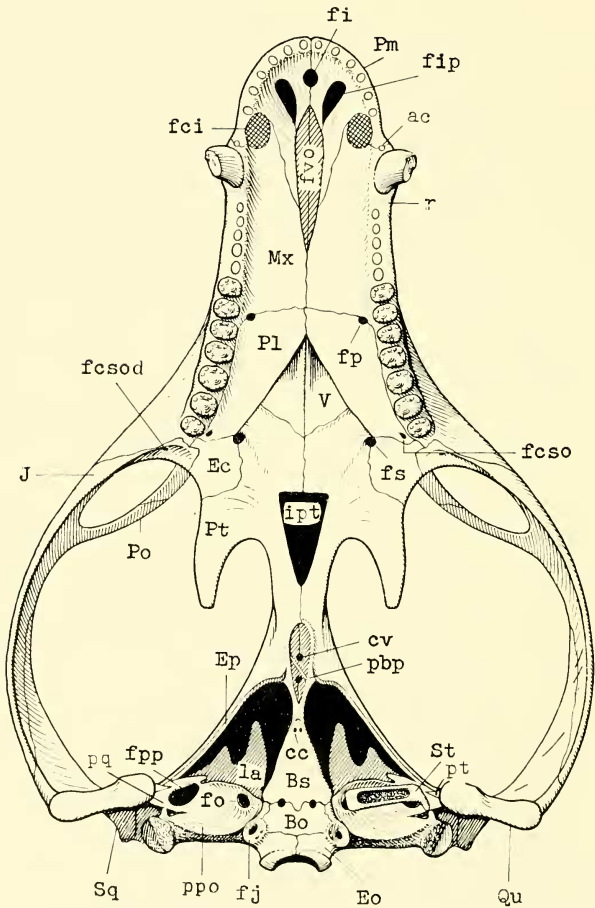
FIG. 2. *Dvinia prima* Amalitzky, ex PIN 2005/2469; ventral view of the skull (× 1.8).

rior edge of the secondary palate is concave. The palatines make up a smaller part of the secondary palate than Konzhukova (1949, Fig. 15) has indicated. A foramen is present within the suture between the palatines and the maxillaries.

Anteriorly in the secondary palate are large apertures for the lower canines(fci), which are located immediately in front of the upper canines and are bordered by the maxillaries and the pre-maxillaries. The latter are deeply incised along their posterior border by a palatine fissure(fip) of the mammalian type. There is also a fairly large foramen incisivum(fi), which is also present in *Diademodon* (Brink, 1955). The medial processes of the premaxillaries form a high wall around the sides of the vomer. The anterior end of the latter, like the internasal septum located on the dorsal surface of the vomer, show clear indications of a paired structure. Among the cynodonts, such a pattern has been observed only in *Cynognathus* (Broili and Schröder, 1934).

It is usually believed that in primitive cynodonts with a complete secondary palate, the palatal fissures grade posteriorly into a large medial fenestra between the maxillae and the vomer (as in *Gale-saurus:* Rigney, 1938; and *Thrinaxodon:* Parrington, 1946a). But in *Dvinia* the area of these foramina is represented only by a deep vacuity with very smooth "polished" walls in the ventral surface of the vomer (see Fig. 2, fvo). The function of this pit, which is described here for the first time in the theriodonts, is not clear. Thus the secondary palate in *Dvinia* is penetrated only by the palatal fissures and the apertures for the lower canines.

The medial and lateral processes of the premaxilla are almost completely separated posteriorly by the palatal fissures, whose ends are separated by only a very small interval. The vomer forms a small paired boss wedged slightly in between these processes and the posteriorly closing ends of the palatal fissures. It is at this very point in *Moschops* (= *Ulemosaurus*) that the vomer is penetrated by the canals of Jacobson's organ (Tatarinov, 1956b). In *Dvinia,* therefore, Jacobson's organ may have opened into the palatal fissure in this area, without however penetrating through the vomer.

The shape of the ectopterygoid is quite different from that shown by Konzhukova (1949, Figs. 4 and 15). This bone, as in the procynosuchids (Brink, 1963b), actually forms the anterior por-

tion of the transverse pterygoid processes and not a narrow projection wedged between the palatine and maxillary bones.

The interpterygoid vacuity(ipt) is triangular in shape, its vertex pointing backward, and is bordered only by the pterygoids. It was noticed in the holotype *"Permocynodon sushkini"* by Sushkin (1927, 1929), but evidently not by Konzhukova. Among all the known cynodonts, the interpterygoidal vacuity occurs only in the Procynosuchidae (Broom, 1938; Brink,1963b), in young individuals of the Galesauridae (*Platycraniellus:* van Hoepen, 1916; *Thrinaxodon:* Estes, 1961) and in *Scalopocynodon* — a peculiar form which links the typical cynodonts with the scaloposaurids (Brink, 1961).

A palatal suborbital foramen (Fig. 2, fs) occurs only in *Scalopocynodon* (Brink, 1961) and perhaps also *Diademodon* (Watson, 1911), apart from the Northern Dvina cynodonts. The so-called "suborbital foramen" described by Broili and Schröder (1934) in the *Cynognathus* palate and in *Diademodon* (Broili and Schröder, 1935) occupies a more lateral position and is bordered externally by the maxillaries and the jugals. In *Dvinia* this aperture coincides with the palatal suborbital foramen and is bordered by the ectopterygoid, the maxillary and the palatine (Fig. 2, fcso). In my opinion, this corresponds to the ventral foramen for the entrance of the suborbital canal in *Moschowhaitsia* (Tatarinov, 1964). The dorsal foramen for the entrance of this canal (fcsod) is located at the bottom of the orbit and is bordered in *Dvinia* by the lacrimal, the maxillary and the jugal. In contrast to *Moschowhaitsia,* the suborbital canal in *Dvinia* is enclosed throughout its length.

In *Moschowhaitsia* the ventral foramen for the entrance of the suborbital canal is bordered, in addition, by the jugal, but in the dorsal foramen for the entrance of this canal the ectopterygoid is separated from the edge of the maxillary (Tatarinov, 1964). In the arrangement of the foramina for the entrance of the suborbital canal and its enclosure along its entire length, *Dvinia* thus somewhat resembles the tritylodonts, in which the dorsal foramen is bordered only by the lacrimals and the maxillaries, and the ventral foramen by the palatinum, the lacrimal and the ectopterygoid (*Oligokyphus:* Kühne, 1956). In other cynodonts (*Cynognathus:* Broili and Schröder, 1934; *Diademodon:* Brink, 1957) the maxillary bone does not extend as far to the rear and

does not reach the edge of the ventral foramen for the entrance of the suborbital canal.

The basipterygoid articulation is immobile. A characteristic feature is the vertical orientation and the closeness of the basipterygoidal processes, which are connected beneath the rostrum of the basisphenoid (Tatarinov, 1966a). No ventral medial contact between the basipterygoid processes is known in other reptiles. Between the basipterygoid processes and the rostrum of the basisphenoid there are asymmetrical (left in front of the right) Vidian canals. Somewhat indistinct sulci which apparently contained the palatal arteries and nerves lead from the foramina for the entrance of the internal carotid arteries in the corpus of the basisphenoid to the Vidian canals. The epipterygoid and the pterygoid are connected by a suture with the external surface of the basipterygoid processes; the articulation with the epipterygoid is immediately dorsal to the area of articulation with the pterygoid.

The pterygoids, which have the form of vertical plates, border the sides of the interpterygoid vacuity laterally, and immediately anterior to the basipterygoid processes they are in contact with each other, without however forming a suture between them. The posterior ramus of the pterygoid is connected with the quadrate, but the epipterygoid evidently terminates at the lateral flank of the prooticum, external to the pterygoparoccipital foramen (Fig. 2, fpp). A similar relationship of the posterior rami of the epipterygoid and the pterygoid with the quadrate has been indicated in the case of *Thrinaxodon* (Parrington, 1946a; Estes, 1961). Thus Sushkin's (1927) and Konzhukova's (1949) statements that there is no contact between the pterygoid and the quadrate bones are in error.

The Occiput

The occipital condyle (Fig. 3, co) is actually double, and not tripartite as Konzhukova wrote (1949). But the two occipital condyles are extremely close and even touching, and the basioccipital in consequence is separated from the edge of the occipital condyle on the ventral surface of the skull (Fig. 3). Such a structure has been found only in *Cynognathus* (Broili and Schröder, 1934) and possibly also in *Glochinodontoides* (Boonstra, 1935).
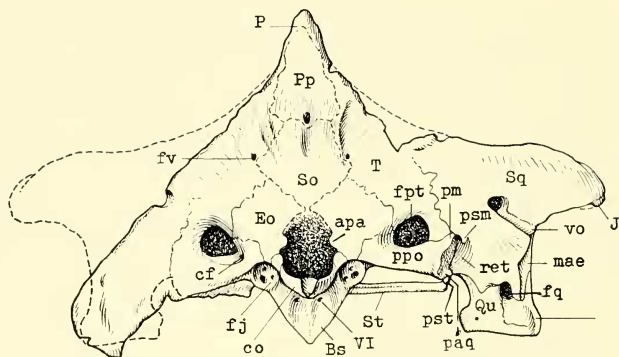
FIG. 3. *Dvinia prima* Amalitzky, ex PIN 2005/2469; occipital view of the skull ($\times$ 2.0).

The exoccipitals are unusually strongly developed, so that they almost meet above the foramen magnum, underlying the supraoccipital; the latter is fairly small, as in *Leavachia* (Brink, 1963b). A dorsal closure of the exoccipital in the theriodonts is described here for the first time. Distinctly noticeable condyles for the neural arches of the proatlas (apa) are developed on the exoccipital along the edges of the occipital condyle. The articulation between these condyles and the proatlas has not been described in the cynodonts, but the neural arches of the proatlases themselves have been illustrated in a similar position in *Leavachia* (Brink, 1963b).

The suture between the tabulars and the squamosals does not lie at the level of the posttemporal fenestra (Konzhukova, 1949), but at a slight distance lateral to the posttemporal fenestra (fpt), at the level of the exterior end of the paroccipital process (ppo). The postparietal, the tabular and the squamosal are all penetrated by several small foramina for blood vessels.

THE REGION OF THE MIDDLE EAR

The two otic bones are completely fused into a typically mammalian periotic, and we can speak only tentatively of any distinction between the prootic and the opisthotic. The positions of the walls of the tympanic cavity are in all probability marked by the

system of ridges on the ventral surface of the periotic. Of these ridges, the posterior runs along the lower posterior edge of the paroccipital process; the relatively short anterior ridge runs anterior to the fenestra ovalis (vestibuli) at the level of the posterior edge of the basisphenoid; and the exterior ridge is represented by the lateral flank of the prootic (Fig. 4). It is interesting that the fenestra rotunda (cochleae)(fr) apparently emerged outside the tympanic cavity, in a deep pit separated by a distinct ridge from the ventral surface of the periotic. The foramina for the exit of cranial nerves IX, X and XII also opened into this pit (Fig. 4). Among the extant tetrapods, this "extratympanic" location of the cochlear fenestra is typical of the anuran amphibians, and also occurs in lizards and monotremes.

The anterior portion of the lateral flange of the prootic bends inward and terminates in a marked distinct "hook" which is separated by a deep incisure from the anterior wall of the tympanic
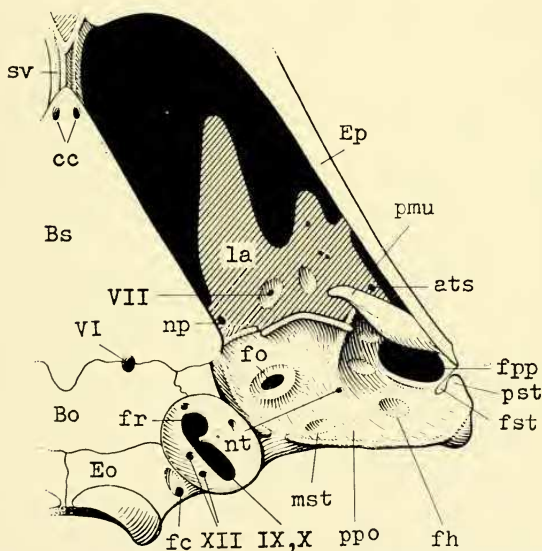

FIG. 4. *Dvinia prima* Amalitzky, ex PIN 2005/2469; ventral view of the otic region ($\times$ 4).

cavity (Fig. 4, pmu). This hook resembles the muscular process of the periotic in the mammals, which borders on the outside the osseous part of the eustachian tube, and may perhaps be analogous to it. If so, the eustachian tube was connected with the middle-ear cavity in the antero-exterior corner of the latter.

For other theriodonts the ridges, which border the tympanic cavity, and the muscular process are unknown. Hopson (1966), using general features of the ear region of the skull as a basis, reconstructed a similar tympanic cavity in cynodont *Thrinaxodon* and in the tritylodont *Bienotherium*, and compared it with those in monotremes *(Ornithirhynchus)*. But Hopson supposed that in theriodonts there was a wide opening between the tympanic cavity and the eustachian tube, as in lizards (Hopson, 1966, Figs. 4c, 6a). The ridges and incisure described in *Dvinia* permit us to believe that in cynodonts the eustachian tube was as narrow as in mammals, and that it opened into the anterolateral region of the tympanic cavity.

The ventral surface of the paroccipital process gives the impression of being spongy, which may be an indication of an incipient development of the air passages (cellulae mastoideae) which are characteristic of the mammals. Posterior and external to the fenestra ovalis (fo) there is a deep fossa (mst) that is comparable to the attachment groove of the M. stapedius in the tritylodont *Oligokyphus* (Kühne, 1956). Kermack (1963), however, suggested that in the triconodonts the end of the cornus hyoideum of the hyoid bone entered a similar pit.

The stapes is a thin-walled bony frame surrounding the very large foramen stapedialis (Sushkin, 1927); Konzhukova (1949) took this foramen to be a shallow pit in the relatively massive stapes. The base of the stapes descends into the fenestra ovalis. The distal end of the stapes terminates without attachment at the level of the end of the paroccipital process and bears a rudimentary spur at the top which merges with a short ventral projection on the paroccipital process (Fig. 3, pst); Sushkin (1927) said merely that the stapes touched the edge of the paroccipital process. A similar projection at the top of the distal end of the stapes has been described in *Thrinaxodon* (Parrington, 1946a; Hopson, 1966); the gorgonopsian *Scylacops* also has such a projection or spur at the top, but this is very massive (Parrington, 1955). Instead of a dorsal (upper) projection, a so-called extrastapedial process has

been described on the stapes in the therocephalian *Lycedops*
(Broom, 1936) and in the cynodont "*Trirachodon*" (*Scalenodon;*
Parrington, 1946a); however, this may be the same as the dorsal
process. In Parrington's opinion (1948), the process on the stapes
of the gorgonopsian *Cyonosaurus* and the pristerognathid thero-
cephalian, which was described by Olson (1944) as an internal
process, should also be considered a dorsal process.

It is commonly believed that the distal end of the stapes in
theriodonts has also the internal (quadrate) process, which
attached to a special process of the quadrate. But hitherto there
has not been described any theriodont with more than one dis-
tinct process on the stapes. In primitive synapsids, in which the
stapes is ossified more completely, the distal end of it reached to
the internal surface (but not to the special process) of the quad-
rate. For *Thrinaxodon*, Hopson (1966) mentioned the "limited
contact" between the distal end of the stapes and the internal
surface of the quadrate. In *Dvinia* the cartilaginous continuation
of the stapes also possibly reached to the internal surface of the
quadrate, and, significantly, above it to the medial condyle. As in
other synapsids (pelycosaurians: Romer and Price, 1940; titano-
suchians: Orlov, 1958; dicynodonts: Camp, 1948) this contact
apparently was a loose one. Descriptions of a firm contact between
the stapes and the quadrate in the dinocephalian *Moschops*
(= *Ulemosaurus*) *svijagensis* (Efremov, 1940) and in the gor-
gonopsian *Sauroctonus progressus* (Bystrov, 1955) are erroneous.
In *M. svijagensis* (Ex. PIN 2207/2) the unusually completely
ossified stapes only touches the quadrate. In *S. progressus* the
distal end of the stapes is not ossified, and on Bystrov's original
specimen (Ex. PIN 156/6) was "reconstructed" with plaster. In
this connection it may be recalled that in crossopterygians the
hyomandibular also lacks a special quadrate process and was
arranged close to the internal and posterior surface of the palato-
quadrate without being in direct contact with it (Jarvik, 1954).

The so-called stapedial process of the quadrate (Olson, 1944),
which Parrington (1946b) calls the pterygoid process, in *Divinia*
(Fig. 2, pt) is slightly bifurcated at the end and contacts the
pterygoid (at the front) and the quadrate process of the periotic
(behind) (Fig. 2, pq). It lies lateral to the pterygo-paroccipital
foramen and anterior to the distal end of the paroccipital process.
Thus the impression is created that the quadrate process of the

periotic in *Dvinia* is formed not by the opisthotic, but by the prootic. Until the present time, among the cynodonts a connection between the quadrate bone and the prootic has been noted only in *Leavachia* (Brink, 1963b). A connection of these bones is also indicated, however, in one illustration of *Diademodon* (Broili and Schröder, 1935, Fig. 31). But according to Crompton (1964), in all cynodonts including *Leavachia* the quadrate is connected not with the prootic, but with the opisthotic. In the scaloposaur *Tetracynodon*, the quadrate process of the periotic clearly has an "opisthotical" origin (Sigogneau, 1963, Fig. 2).

The quadrate process of the periotic in cynodonts, whatever its composition, is apparently an evolutionary novelty. In some primitive theriodonts, as in *Sauroctonus progressus*, this process is lost. In crossopterygians the palatoquadrate also lacks a direct connection with the otic capsule (Jarvik, 1954).

The External Auditory Meatus

Running along the outer edge of the occipital surface of the squamosal in *Dvinia* is a narrow groove (Fig. 3, mae) which begins at the lower end of the jugal process of the squamosal. This groove terminates above the lateral condyle of the quadrate bone, directly medial to the processus ascendens of the quadrato-jugal. The groove described here is very similar to the so-called external auditory meatus of *Oligokyphus* (Kühne, 1956, Fig. 10) and is without any doubt homologous to it. The similarity of these structures is underlined by the identical nature of their relationship to the articulating surface of the processus ascendens of the quadratojugal: the latter has the form of a groove that becomes increasingly sharp upwards, separated from the lower part of the external auditory meatus only by a barely discernible ridge. In that case, however, just as in *Oligokyphus* the upper end of the external auditory meatus terminates freely at the jugal process of the squamosal, in *Dvinia* this meatus is closely connected with a transverse venous groove (vo) in the occipital surface of the squamosal and even appears to branch off from the latter. The transverse venous groove in *Dvinia* runs from the lower end of the jugal arch to a foramen in the squamosal located exterior to and above the posttemporal fenestra. Its position shows a strong resemblance to the passage of the occipital vein and

artery in the monotremes (the echidnas), which also pass through the squamosal (Hyrtl, 1853; Hochstetter, 1896). In all probability, in *Dvinia,* too, the transverse groove contained the occipital vein (and artery).

At first glance, the connection between the groove of the external auditory meatus and the occipital vein in *Dvinia* would seem to cast doubt on the correctness of this interpretation. It seems at least possible that the "external auditory meatus" of *Dvinia* actually contained the large vein which connected the occipital vein with the vena capitis lateralis or with the vena jugularis interna. It must be remembered, however, that it is precisely in the echidna *Tachyglossus* that there is a close topographic connection between the external auditory meatus and the occipital vein. The external auditory meatus in the monotremes has the form of a long cartilaginous tube which opens in the postorbital region (Denker, 1901). From here the cartilaginous auditory meatus runs above the jugal arch to the occiput, where it makes a sharp downward turn. In *Tachyglossus,* at the point of this sharp turn the auditory meatus almost touches the occipital vein (Hochstetter, 1896).

The general similarity of the topographical relationships of the various grooves in the squamosal in *Dvinia* to the occipital vein and the auditory meatus in the echidna cannot be doubted. Therefore the hypothesis according to which a cartilaginous auditory meatus ran along the vertical groove in the squamosal of *Dvinia* seems to the present writer to be closer to the truth than the supposition that this groove was connected with the vein.

In *Oligokyphus* there appears to have been no groove for the occipital vein, but the turning of the external auditory meatus at the outer surface of the jugal arch is quite distinct. The external auditory meatus also shows a similar development in other tritylodonts (*Bienotherium:* Hopson, 1966, Fig. 6) and in the higher cynodonts — the representatives of the Cynognathidae, the Diademodontidae and the Traversodontidae (infraorder Cynognathia, according to Brink, 1963c). In all these cynodonts the groove through which the external auditory meatus ran is considerably wider than in *Dvinia* and *Oligokyphus,* and at the top it emerges directly at the external surface of the jugal arch. No groove for the occipital vein has been found either in the higher cynodonts or in any other theriodonts, but it must be noted that among the

monotremes also, the occipital vein is not developed in the platypus (Hochstetter, 1896).

The suggestion that the groove in the squamosal of the higher cynodonts contained the external auditory meatus was made at almost the same time by W. K. Gregory (1910) and D. M. S. Watson (1911). Both these authors compared the cynodonts with the placentals and the marsupials, which have a relatively short external auditory meatus which typically leaves a distinct impression on the squamosal. The analogy with the Monotremata would seem to be contradicted by the specialization of the external auditory meatus in the latter, which moreover leaves no traces of its existence on the bones. Even the origin of the cartilaginous tube of the monotremate auditory meatus is obscure; it has been suggested that its development was associated with the secondary adaptation of the monotremes to a burrowing or aquatic way of life (Gregory, 1947). But a study of *Dvinia* seems to show that a direct comparison of the external auditory meatus between the cynodonts and the Monotremata may be justified; a similar conclusion was reached by Hopson (1966). In this regard, the only important difference between these two groups of animals is the lack of any connection between the cartilaginous auditory tube and the cranial bones in the Monotremata. On the other hand, the comparatively simple auditory meatus in the marsupials and the placentals occupies a rather different position and can scarcely be compared to the auditory meatus in the monotremes and the cynodonts (Kühne, 1956). It is worth mentioning especially that in the marsupial and placental mammals the external auditory meatus has the form of a short transverse tube located immediately behind the mandibular articulation; moreover, in the ictidosaurs *(Diarthrognathus)* the new mandibular articulation is formed lateral to the area of the pterygoparoccipital foramen (Crompton, 1958, Fig. 1) — that is, at a considerable distance from the cynodont auditory meatus.

The problem of the external auditory meatus in the lower cynodonts, as well as in other groups of theriodonts, still remains obscure. Among the lower cynodonts, a typical groove-like auditory meatus is known only in *Dvinia*. In other primitive theriodonts the "external auditory meatus" is represented by a very large triangular area in the occipital surface of the squamosal. On its external side this area has no clear boundaries, but it is

bordered on the internal side by a ridge of the squamosal contact of the latter with the paroccipital process. Such an "auditory meatus" has been described in the primitive cynodonts (Brink, 1963b; Crompton, 1964), the bauriamorphs (Brink, 1963a), the scaloposaurids (Crompton, 1955a; Sigogneau, 1963), the gorgonopsids (Pravoslavtsev, 1927) and even the dinocephalian *Moschops* (= *Ulemosaurus*) (Parrington, 1955). In one form the picture (Fig. 4) this "groove" is bordered by the squamosal seems to occur in all the therapsids. It appears doubtful to the present writer, however, that this is directly comparable to the external auditory meatus of the higher cynodonts and *Dvinia*. Recently a groove for the external auditory meatus was described in the primitive cynodont *Thrinaxodon* (Hopson, 1966). But in the picture (Fig. 4) this "groove" is bordered by the squamosal crest only on the inner edge, and, as is common in primitive theriodonts, there is not a great difference between it and a depression on the occipital surface of the squamosal.

The area on the occipital surface of the squamosal in the therapsids seems to have served as the attachment area for the M. depressor mandibulae. The development of this muscle in the theriodonts is testified, in particular, by the presence of a distinct retroarticular process (Crompton, 1963a, 1963c). The area on the squamosal is located exactly above the mandibular articulation, and may very well have been used by the muscle which opened the mouth. It is well known that in the mammals the M. depressor mandibulae was reduced and was replaced functionally by a new muscle for opening the mouth — M. detrahens mandibulae in monotremes and M. digastricus in other mammals. Watson (1953) states that an external auditory meatus was formed only in the higher cynodonts, and he associates its formation with the reduction of the M. depressor mandibulae. According to this view the external auditory meatus was formed in that area of the squamosal which had previously been covered by the M. depressor mandibulae. But in *Dvinia,* in which, judging by the strongly developed occipital surface of the squamosal, the M. depressor mandibulae did not undergo reduction, the groove for the external auditory meatus is not only very distinct but is also spatially separated from the probable place of attachment of the muscle for opening the mouth; the latter seems to have been a shallow and somewhat irregularly shaped pit located on the squamosal medial

to the auditory meatus, exactly above the area of the mandibular articulation.

The narrow, trough-like auditory meatus of the *Dvinia* type may also have been possessed by other primitive cynodonts of the infraorder Procynosuchia, and may be discovered in them too as a result of more careful preparation of the occipital area. It should be recalled in this connection that the very distinct auditory meatus of *Dvinia* was not noticed by the authors who previously described this cynodont (Sushkin, 1927, 1929; Konzhukova, 1949). The external auditory meatus should be sought not at the contact of the squamosal with the paroccipital process, where Parrington (1955) and Hopson (1966) have reconstructed it, but much further to the side, below the base of the jugal process on the squamosal. It should be noted that in the gorgonopsids, at least, there was evidently no groove for the external auditory meatus on the squamosal, as indicated by the present writer's study of the beautifully preserved materials of the Late Permian *Sauroctonus progressus* which are in the Paleontological Institute of the Academy of Sciences of the U.S.S.R. (Specimens PIN 156/6, 156/7, and 156/57).

The Problem of the Location of the Tympanum in Theriodonts

There are four alternative hypotheses on the location of the tympanum in theriodonts:

1. In all synapsids the tympanum was located in typical "reptilian" position behind the quadrate. It is homologous to the tympanum of all other tetrapods. But in synapsids, together with the closure of the otic notch, the tympanic membrane migrated medially to a position above the medial condyle of the quadrate. This displacement is related to the formation of the external auditory meatus (many authors, especially Parrington, 1948, 1955).

2. At least in theriodonts the tympanic membrane was located in the "pro-mammalian" position — in the concave posterior border of the reflected lamina of the angular. A special ventral recess of the tympanic cavity extends to this region. When a new jaw articulation was established in the mammalian ancestors, the

postdentary bones of the lower jaw were pulled into the tympanic cavity (Palmer, 1913).

3. The therapsids had two tympani: the ancient (reptilian) attached to the back of the quadrate, and the new in the concave posterior border of the reflected lamina. The new tympanum appeared for the first time in the sphenacodont pelycosaurs, which had a reflected lamina. In mammals both tympani were brought together and united. The reptilian tympanum formed the pars flaccida (membrana Shrapnelli) of the compound mammalian tympanum (Westoll, 1944, 1945).

4. The primitive synapsids did not have a tympanum at all. The progressive cynodonts acquired a new (mammalian) tympanum, located in the concave posterior border of the reflected lamina, which is not homologous with the tympanum of all other tetrapods. Behind, the new tympanum may reach to the stapes and the region of the jaw articulation. Formation in the cynodonts of the external auditory meatus is related to the transformation of the jaw articulation and to reduction of the depressor mandibulae muscle. (Tumarkin, 1948; Watson, 1951, 1953, 1954).

In the past I supported the fourth hypothesis, and, following Tumarkin, considered the lack of a tympanum in primitive synapsids as the initial condition (Tatarinov, 1958), but not the secondary one, as Watson thought. Now I think that the typical therapsids had a tympanum. But it is doubtful that in therapsids the tympanum was located on the back of the quadrate. In this connection the structure of the ear region in *Dvinia* is significant.

It has usually been supposed that in the therapsids the eardrum was located between the medial condyle of the quadrate bone and the lower edge of the squamosal or the opisthotic (Parrington, 1948, 1955, 1958; Cox, 1959); the external auditory meatus in the higher cynodonts ran directly to the medial condyle. But in *Dvinia,* because of the elongation of the quadrate process of the squamosal, the mandibular articulation was much lower down and the medial condyle of the quadrate bone is some distance from the edges of the opisthotic and the squamosal (see Fig. 3). For this reason, apparently, Gregory reconstructed the tympanum in *Cynognathus* in the "usual" location, but in *Dvinia* placed it in between the medial condyle and the lower edge of the artic-ular bone of the mandible (Gregory, 1951, Vol. 2, XVI, Figs. 53 & 54) — a position which is highly tentative. It is significant

that the external auditory meatus runs along the external (but not internal) edge of the squamosal in *Dvinia*. The possibility of the connection of this auditory meatus with the region between the paroccipital process and the medial condyle of the quadrate is extremely questionable.

The tympanum in *Dvinia* also cannot have been attached to the incisure between the squamosal and the paroccipital process, which Broom (1936) believes supported the upper edge of the tympanum in the therocephalian *Lycedops;* suffice it to say that in *Dvinia* this incisure is completely closed off at the bottom (see Fig. 3, ret). The formation of this incisure, which in *Dvinia* rather has the form of a deep fossa, is due to a posterior projection of the paroccipital process and the incomplete ossification of its external margin. Incomplete ossification of the end of the paroccipital process has also been noted in *Leavachia* (Brink, 1963b) and in the scapolosaurids (Watson, 1931; Crompton, 1955a). As in the latter, there are slight upper ("mastoid") and lower ("quadrate") protrusions at the end of the paroccipital process (Fig. 3, pm, paq), but in *Dvinia* they are both connected with the squamosal. The latter in turn forms a small mastoid protrusion (psm) which projects rearward at the upper edge of the incisure. The tympanum, if *Dvinia* had one at all, would have been located in the incisure between the paroccipital process and squamosal, would have been underlain by cartilage (incomplete ossification of the paroccipital process), and would have been separated from the distal end of the stapes (see Fig. 3). For these reasons *Dvinia's* eardrum could not have been located in the incisure at the outer end of the paroccipital process, where it has been reconstructed in the tritylodont *Oligokyphus* by Kühne (1956). It seems more likely that in life the pit between the paroccipital process and the squamosal, as in many mammals, received the cornus hyoideum of the hyoid bone, which would have been fused with the paroccipital process.

In the triconodonts, which in the structure of the otic region of the skull had much in common with the tritylodonts, the tympanum may have been attached to a ventral projection of the paroccipital process, which resembles the tympanic process in the cranium of the Monotremata (Kermack, 1963). In the tritylodonts the distal end of the paroccipital process is expanded anteroposteriorly and divided into two prominent projections, of

which the anteroventral is very massive (*Oligokyphus:* Kühne, 1956; Crompton, 1964; *Bienotherium:* Hopson, 1964b, 1966). Kühne supposed that the anteroventral projection was connected with the cornus hyoideum, and the tympanum was attached to the edge of the paroccipital process between both projections. But it is more likely that the anteroventral projection supported the quadrate bone; the posterior projection may be compared with the mastoid process of mammals (Crompton, 1964). Hopson (1966) agreed with this; he compared the anteroventral projection with the crista parotica in monotremes (and triconodonts), and notes that in *Bienotherium* it carries a medial process which is comparable with the hyoid process on the crista parotica in monotremes.

Therefore it is possible that in tritylodonts some part of the tympanum was attached to the anteroventral projection. But the supposition of Crompton (1964) that the anteroventral and posterior projections may be compared, accordingly, with the quadrate and mastoid process of the paroccipital in cynodonts is doubtful. In *Dvinia* the quadrate process (Fig. 3, paq) is united by a suture with the squamosal and has connections neither to the quadrate nor to the stapes. It is doubtful also that the anteroventral projection of tritylodonts may be compared with the quadrate process of the periotic, which in *Dvinia* is located anterior to the paroccipital (Fig. 2, pq). In this case the posterior process of tritylodonts may be compared with the whole distal end of the paroccipital process of *Dvinia*. But in some scaloposaurians, such as Russian *Chthonosaurus,* the distal end of the paroccipital process is divided as in tritylodonts. In any case *Dvinia,* as distinct from tritylodonts, triconodonts and monotremes, has no sign of the attachment of the tympanum to the quadrate process of the periotic. It is possible that the tympanum acquired this attachment only in tritylodonts.

Thus not one of the locations posterior to the quadrate in which the tympanum has been reconstructed in other theriodonts was suited for this purpose in *Dvinia*. This puzzle is emphasized by the fact that in *Dvinia* the groove of the external auditory meatus disappears above the lateral condyle of the quadrate — a significant distance from any possible position of the tympanum. It is quite possible, however, that the tympanum had one of the following locations: 1) It may have been located posterior to

the mandibular articulation at the end of the cartilaginous tube of the external auditory meatus and behind the depressor mandibulae muscle; it was not attached directly to the cranial bones; there is a possibility that in tritylodonts the tympanum did not have the attachment to the quadrate as noted by Hopson (1966). 2) The tympanum in *Dvinia*, as in other theriodonts, may have had a "promammalian" position, in the reflected lamina of the angular, as first suggested by Palmer (1913). The angular is in all probability homologous with the ectotympanic of mammals.

No final answer can yet be given to the question of where the eardrum was located in *Dvinia* (and other theriodonts). The hypothesis which located the tympanum in the theriodonts posterior to the quadrate bone offers great possibilities for comparison of the the structure of the middle ear between the therapsid and the sauropsid reptiles. But in this case the transition from the theriodont to the mammalian middle ear remains little understood: the stapes must have lost its junction with the tympanum and the articular must have acquired it. Westoll's hypothesis does not give any reasons for the appearance in synapsids of a new tympanum, which must have co-existed with the ancient tympanum. Palmer's variant at first glance seems quite unlikely in view of the obvious impossibility of any direct connection between the stapes and the reflected lamina of the angular (Romer and Price, 1940), and at the present time this hypothesis is rejected by the majority of investigators. It is less likely that the tympanum would have extended from the reflected lamina as far as the medial condyle of the quadrate bone and have been connected at that point to the stapes, as Watson (1951, 1953) suggested. If that were so, in *Dvinia*, for example, the length of the eardrum would have been one fifth that of the whole skull. It seems both wrong and unneccessarily complicated to suppose that the external auditory meatus ran from the jugal arch to an angular tympanum across the occipital surface of the cranium. Finally, an angular tympanum is scarcely comparable to the sauromorph type located in the incisure in the quadrate, and in this case we should probably have to conclude that the eardrum originated independently in the theromorphoid and the sauromorphoid reptiles.

Palmer's hypothesis does, however, have a number of important advantages. Above all, it is only from the theriodont middle ear with an angular tympanum that the mammalian middle ear, includ-

ing the quadrate and articular transformed into ear ossicles, could have been easily derived. The connection between the "promammalian" tympanum in the angular and the stapes may have been formed by the cornus hyoideum of the hyoid bone, which would then have played the role of an extra stapes (Tatarinov, 1965b); in embryos the cornus hyoideum is often connected with the stapes, and among the now extant reptiles, *Sphenodon* has a cartilaginous direct connection between the stapes and the cornus hyoideum which is retained throughout life. If these assumptions are made, Palmer's hypothesis may be quite plausible.

The Lower Jaw

In its main features the mandible of *Dvinia* is typical of the primitive cynodonts of the infraorder Procynosuchia; it has much in common especially with the lower jaw of the archaic cynodont *Leavachia* (Brink, 1963b; Crompton, 1963a). The postdentary bones of the lower jaw in *Dvinia* are not reduced. The reflected lamina (Fig. 5A, rl) of the angular is wide, and extends posteroventrally. The coronoid process (pc) is relatively short and scarcely extends beyond the level of the upper edge of the jugal arch. The area for insertion of external adductor musculature on the lateral face (mt) occupies only the upper part of the coronoid process. In this regard *Dvinia*, like *Leavachia*, differs from the more progressive *Thrinaxodon* (Crompton, 1963a). The area served as a point of insertion for the masseter muscles according to Konzhukova (1949), and for the M. masseter profundus according to Crompton (1963a, 1963c). But in *Dvinia*, when the jaws were closed, this muscle attachment area lay mainly inside (but not downward from) the jugal arch — the possible area of origin of the masseters — and therefore was not much adjusted for receiving these muscles; apparently only the temporal muscle was attached to this area. Another external adductor area in *Dvinia* was bordered principally by a small thickened ridge along the upper edge of the surangular (maep). As in *Leavachia* (Crompton, 1963a), this ridge in *Dvinia* grades into the coronoid process, isolating the lower portion of the muscle attachment pit; it is possible that the most posterior fasciculus of the adductor externus musculature was attached to it. The weak jugal arch of *Dvinia* does not show any distinct signs of areas of muscle origins. As

shown by Barghusen (1968), in primitive cynodonts the masseters had not yet been differentiated. In the progressive cynodonts the attachment area of the developing masseter muscle extended along most of the coronoid process.

The area on the angular portion of the dentary bone and on the reflected lamina, on which Crompton (1963c) reconstructed the attachment of the superficial masseter muscle in other cynodonts, probably did not receive any muscle at all (Barghusen, 1968). In *Dvinia* this area ("mms") is very faintly outlined and did not extend to the reflected lamina, from which it is separated by a ridge developed along the anterior edge of the angular (Fig. 5A, cra). External to the labial surface of the lower postcanine teeth there is a horizontal shelf (hs) which begins at the level of the fifth postcanine tooth and terminates at the base of the coronoid process.

The adductor fossa between the surangular and the prearticular is well developed (Fig. 5B, fa). In the posterior part of the prearticular there is a foramen for N. chorda tympani (fch). The coronoid, which forms the anterior border of this fossa, extends forward to the level of the ultimate postcanine tooth. There is also an anterior coronoid which is preserved only on the left side. This bone is located above the splenial and in front reaches the level of the sixth postcanine tooth. An anterior coronoid bone has been described in the theriodonts thus far only in *Leavachia* (Brink, 1963b). Konzhukova (1949) did not describe the coronoids in *Dvinia*, but Sushkin (1929) noted the presence of the posterior coronoid.

The mandibular symphysis, which is formed by the dentaries and the splenials, is very thick and runs back obliquely to the level of the fourth postcanine tooth. The precanine part of the dentary projects forward, and is distinct from the main part of the jaw. This peculiarity imparts a somewhat beak-like appearance to the lower jaw.

The foramina for the blood vessels and nerves in the anterior part of the lower jaw and presumably for innervation of the lower lips (fm) are more numerous than similar foramina in the maxilla and premaxilla. One small foramen opens externally at the base of each of the incisors except, apparently, for the fifth incisor; the largest of these foramina are the most anterior and the most posterior. Three larger mental foramina are present
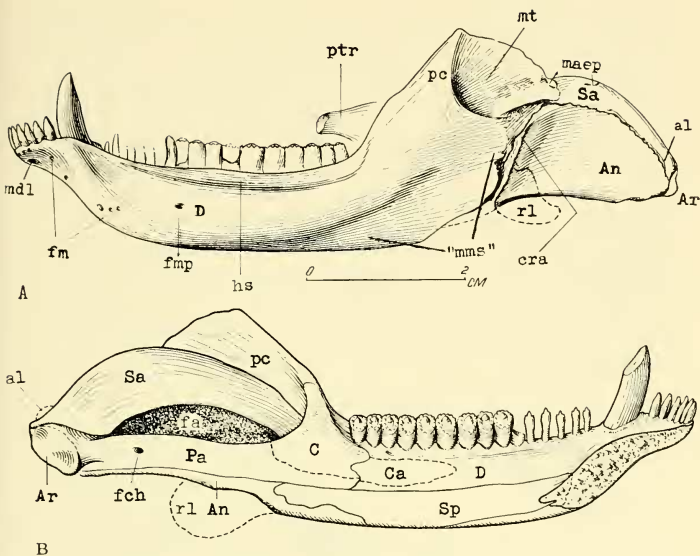
FIG. 5. *Dvinia prima* Amalitzky, ex PIN 2005/2469; lower jaw: A — external view; B — internal view ($\times$ 1.8).

at the posterior base of the canine. The largest is the posterior mental foramen (fmp), which emerges at the level of the sixth postcanine tooth (Fig. 5A). In comparison with the more primitive theriodonts, there is a tendency toward a posterior migration of the mental foramina. This is probably due to the development of musculature for the lower lip. Another indication of the existence of such a lower lip is the groove-like muscle impression of the M. depressor labii inferioris or the M. mentalis (mdl), which occurs on the mental projection below the bases of the second to fourth incisors and lower than the anterior mental foramina (Tatarinov, 1967).

THE MANDIBULAR ARTICULATION

The area of the mandibular articulation in *Dvinia* is displaced downward considerably from the exterior end of the paroccipital

process, and is located a little below the level of the occipital
condyle. As a result, the angle of attachment of the temporal
muscle is larger and the force which it developed in the adduction
of the jaws was increased (Tatarinov, 1966b). The quadrate and
the quadratojugal bones are comparatively massive and close
together. A foramen (Fig. 6, fq) is present between the quadrate,
the upper edge of the quadratojugal, and the processus ascen-
dens (pas) of the quadratojugal. In addition, within the quadrate
bone itself, just above and behind the medial condyle, a small
foramen opens posteriorly (fqa). Contrary to Konzhukova's asser-
tion (1940), both the medial and the lateral condyles of the
mandibular articulation are formed by the quadrate bone and not
by the quadratojugal, as in *Thrinaxodon* (Parrington, 1946b).
The exterior side of the quadrate in *Dvinia* bears a process which
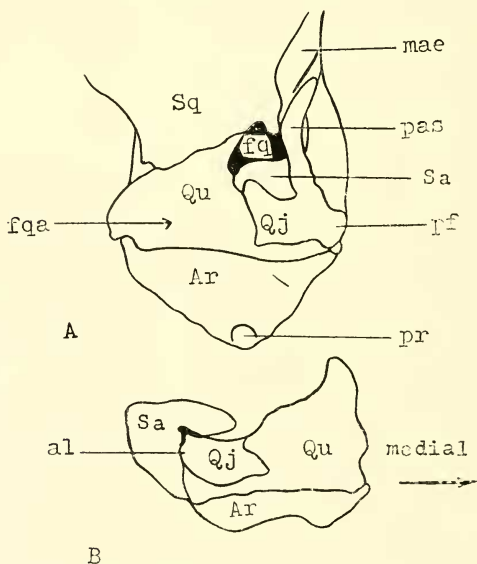underlies the quadratojugal. The retroarticular process of the

ı ıɢ. 6. *Dvinia prima* Amalitzky, ex PIN 2005/2469; mandibular articula-
tion region: A — rear view, right side (× 4.0); B — in transverse section,
left side (× 4.0).

lower jaw (pr) is not preserved on the left side, and is very damaged on the right.

Sushkin (1929) noted that the articulation of the lower jaw with the skull involves not only the articular (and quadrate), but also the surangular and quadratojugal. Konzhukova (1949) said, however, that this observation of Sushkin's was in error and that the holotype *"sushkini"* had a primitive, normal reptilian mandibular articulation. In reality, the mandibular articulation of *Dvinia* is unusually complicated and appears to have been double (Tatarinov, 1966b). The surangular, which is thickened posteriorly, articulated with the exterior edge of the quadratojugal (Figs. 5B, 6B: al). The quadratojugal at this point forms a falciform projection, which touches for a limited distance the inner surface of the surangular (Fig. 6, pf). Details of this articulation are unclear because of the conditions of preservation, but there is little doubt of its existence. In addition, the thickened posterior edge of the surangular projects inward for almost half the distance between the lateral and the medial condyles of the quadrate bone, and almost reaches the anterior edge of the quadratojugal (Fig. 6B). The purpose of the supplementary articulation was apparently to have prevented any lateral or anteroposterior movement of the lower jaw. As the mouth was opened, the articulating surface of the surangular slid downward and slightly forward along the quadratojugal. The amplitude of this movement was, of course, not very large because of the close proximity of the supplementary and main articulations.

DENTITION

The dental formula of *Dvinia* is as follows: I 5 - 6/6; C 2/1; Pc 12 - 13/15. The rudimentary anterior canine (Fig. 2: ac) in the upper jaw, of which only the alveoli are preserved, was not mentioned by Sushkin (1929) or Konzhukova (1946a, 1949). Both these authors described 12 postcanine teeth in both the upper and lower jaws of the holotype *"sushkini"*, but the full complement of teeth in the lower jaw could only be determined after additional preparation. In the case of the upper jaw it is still not clear whether there were 12 or 13 postcanine teeth, since behind the functioning canine on the left side the probable remains of a tooth are present. Hence it is not impossible that the foremost

postcanine tooth in *Dvinia* was shed in life to make room for the growing canine, as in *Thrinaxodon* (Hopson, 1964a). In the case of PIN 2005 2465, it is reliably established that 13 teeth were present in the upper jaw. From the conditions of their preservation, it is unclear; there may or may not have been a rudimentary anterior canine in the holotype of *Dvinia*. The incisors in this specimen of *Dvinia* have not been preserved.

The incisors in *Dvinia* have blunt conical shapes. The canines are highly compressed laterally. The postcanines are sharply differentiated into conical "premolars" (I - VI) and transversely widened "molars" (VII - XV) which have numerous additional cusps. On the upper "molars" the additional cusps are ranged along the edges of the crowns around the highly developed principal cusp, whereas on the lower "molars" the additional cusps are arranged roughly in three transverse rows. In all these features the teeth of the Northern Dvina cynodonts show a definite similarity to the transversely widened teeth of the Triassic cynodonts of South Africa and South America (Crompton, 1955b; Romer, 1961; Bonaparte, 1963b). In contrast to the latter, however, the crowns of the lower teeth in *Dvinia* did not occlude with the uppers when the jaws were closed, but lay inside and slightly forward of the latter. In this respect *Dvinia* retained some resemblance to the primitive theriodonts with non-occluding dentition. The presence of this occlusion was illustrated by the fitting of the lower canines of *Dvinia* to the palatal vacuities for their reception and the middle of the lower jaw against the pterygoid flanges.

Nevertheless, the postcanine teeth of Dvinia were "grinding" teeth. The food was pressed by the lower postcanines against the secondary palate and by the upper postcanines against the horizontal shelf of the lower jaw, outside the postcanine teeth (see Fig. 5A, hs). (It should be noted that such use of the horizontal shelf is possible only if the animal has cheeks to contain the food. This is indirect confirmation of the present writer's inference that the cynodonts developed the rudimentary cheeks and lips typical of mammals |Tatarinov, 1967|.) The development of such an apparatus for grinding food shows signs of what V. O. Kovalevskiy has termed "inadaptive specialization." The two rearmost lower teeth have no opposites at the top and are located close behind the secondary palate; these teeth pressed the fodder against the transverse process of the pterygoids and against the

ectopterygoid (see Fig. 5A, ptr). In other theriodonts more post-canine teeth have sometimes been counted in the lower jaw than in the upper. In these, however, the "excess" postcanines were evidently front teeth. In the case of *Thrinaxodon,* at any rate, it has been shown that when the jaws were closed, the additional teeth in the lower jaw lay medial to the upper canines (Hopson, 1964a).

Konzhukova stated, however, that the crowns of the postcanine teeth occluded in *Dvinia,* and that this was indicated by the presence of distinct wear facets on the teeth on the lingual half of the upper "molars." The less prominent wear facets on the labial side of the upper postcanines were, according to Konzhukova, due to abrasion by the food rather than occlusion. Actually, however, the wear facets described by Konzhukova (1949) are areas damaged during preparation. The cusps on the "molars" are very brittle. In reality, because of the lack of occlusion the "molars" generally are scarcely worn at all. This was confirmed by a study of the previously unprepared crowns of molars in the holotype of *"P. sushkini."* Konzhukova (1949) correctly noted that lateral grinding movements of the lower jaw were impossible, but she assumed that limited anteroposterior move-ments were possible. As I have already indicated, the nature of the mandibular articulation eliminates the possibility of either transverse or propalinal movements of the lower jaw.

THE POSTCANINE TEETH

The crowns of the postcanine teeth are covered with longitudinal furrows. Up to the present, such furrowing has been noted in the cynodonts only in the galesaurid *Nanictosuchus melinodon* (Broom, 1940), but I have seen it also in a new galesaurid *Nanocynodon seductus* (Tatarinov, in press). The furrowing of the enamel does not signify the initial stage of development of additional cusps as supposed by Konzhukova (1946b, 1949). In the holotypes of *"Permocynodon sushkini"* and *Dvinia prima* furrowing of the enamel appears on both the "premolar" teeth which have no additional cusps as well as the "molars," which have well developed additional cuspules.

A clear differentiation of the postcanines into "premolars" and "molars" was noted in the holotype *Dvinia prima* by Amalitzky

(1922), but was not adequately stressed in the descriptions of the holotype *'Permocynodon sushkini*" by Sushkin (1929) and Kon-zhukova (1946b, 1949). Sushkin stated only that the post-canines gradually become more complicated from front to rear.

In both the upper and the lower jaws, the "premolars" are circular in cross section. Only the posterior of these has two additional cusps — an anterior and a posterior cusp. The holotype of *Dvinia prima* and the lower jaw of the holotype *"sushkini"* had six premolars, but in the upper jaw in the holotype *"sushkini"* there may have been only five such teeth. Yet the first "premolar" in the upper jaw of the holotype *"sushkini"* may have been displaced by the growing canine, so that the total number of premolars in both jaws of *Dvinia* would have been equal at six. Since the left side of the upper jaw of the holotype *"sushkini"* retains signs of a resorbed root of an anterior postcanine tooth, which had been located somewhat inside the posterior edge of the root of the canine, we shall assume henceforth that both specimens of Northern Dvina cynodonts had six "premolars."

The poor state of preservation of the "molars" makes it possible to describe only the general features of the arrangement of additional cusps on them. The upper "molars" (Fig. 7) have a well developed principal cusp located in the center of the crown. The additional cusps are along the edges of the crown, chiefly along the anterior and posterior edges. The number of additional cusps on the upper "molars" in both *Dvinia* specimens varies from 6 to 9 or 10 on each crown (the presence of the external and internal edges of the crown is not established for all teeth). According to Amalitzky, the number of additional cusps on each of the teeth of the holotype of *D. prima* was 9 (on VII - XII) or 6 (on XIII), but Konzhukova said that this number varies in the holotype *"sushkini"* from 4 to 8. After comparing my own data with Konzhukova's description, I believe that she understated the successive numbers of the molars in the holotype *"sushkini"* by one.

The foremost (VII in the present writer's interpretation) and the rearmost "molar" in both specimens of *Dvinia* are approximately square in cross section, while the rest are rectangular and widened transversely. The seventh upper postcanine has 6 additional cusps (9 according to Amalitzky, 4 according to Konzhu-kova), of which 2 are located on each of the anterior and poste-
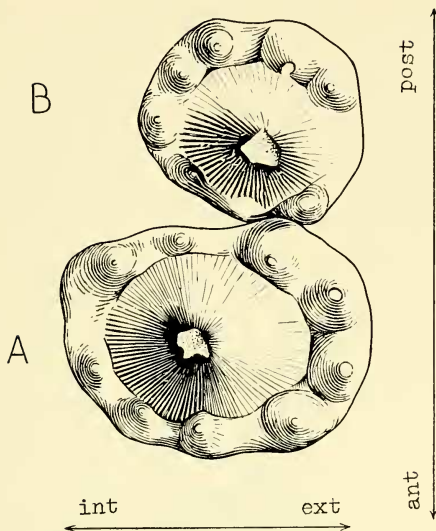
FIG. 7. *Dvinia prima* Amalitzky, ex PIN 2005/2469; upper postcanine teeth; A — 12th tooth; B — 13th tooth, right side ($\times$ 18).

rior edges of the crown and one each on the internal and external edges. The eighth and ninth each have 8 additional cusps (3 each in the anterior and posterior rows and 1 each along the inner and outer edges of the crown), the twelfth (Fig. 7A) has 9 (3 in the anterior, 4 in the posterior and 1 each along the inner and outer edges of the crown), while the tenth and eleventh evidently had 10 additional cusps each (4 each in the anterior and posterior rows and 1 each on the inner and outer edges of the crown). The rearmost tooth (the thirteenth) in the *"sushkini"* holotype appears to have had 8 additional cusps somewhat irregularly placed (3 in the front row, 4 in the rear row and 1 on the inner edge of the crown — see Fig. 8B), but in the *D. prima* holotype and in Specimen PIN 2245/237 the rearmost "molar" tooth evidently has 6 additional cusps. According to Konzhukova (1949) VIII and IX in the *"P. sushkini"* holotype have no more than 5 additional cusps each, XI has 8 and XII evidently

has 6. But the smaller numbers reported by Konzhukova are due to her overlooking the damage to the lingual sides of the teeth which occurred during preparation.

The lower "molars" of *Dvinia,* which are described here for the first time, differ sharply from the uppers. The principal cusp on the lower "molars" is blunted, so that it rises barely above the additional cusps, and is placed at the outer edge of the crown. Thus in the lower "molars" the crown grew inward from the principal cusp. This is clearly due to inadaptive specialization of the *Dvinia* dentition, in which the lower "molars" pressed not against the upper teeth but against the secondary palate. The grinding surface of the crown in the lower "molars" is flattened and has numerous additional cusps arranged roughly in three transverse rows. The total number of additional cusps on each such tooth varies from 8 to 21 (Fig. 8).

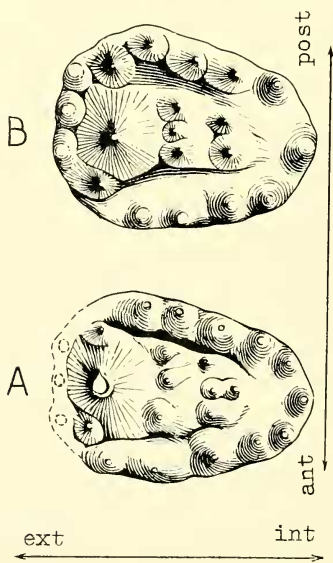In the lower jaw all the "molars" are transversely widened,

FIG. 8. *Dvinia prima* Amalitzky, ex PIN 2005/2469; lower postcanine teeth: A — 11th tooth; B — 13th tooth, right side ($\times$ 15).

especially X - XIV. The seventh postcanine tooth has a total of 8 additional cusps arranged approximately as on the eighth upper postcanine. The arrangement of the additional cusps in three rows on this tooth is only conjectured, and the crown shows relatively little transverse widening. These features suggest that the lower postcanine VII is intermediate between the "premolars" and the "molars." VIII and XV each have 11 additional cusps: 4 each in the anterior and posterior rows and 3 in the middle row (1 external and 2 internal to the principal cusp). Tooth IX has 14 or 15 additional cusps: 5 each in the anterior and posterior rows, 1 external to the principal cusp and 3 or 4 internal to it. The pair of additional cusps directly internal to the principal cusp is arranged in one front-to-rear row. Teeth X and XII - XIV each have 19 additional cusps — 6 each in the anterior and posterior rows, 1 on the outer side of the principal cusp and 5 along its inner side. Here, directly internal to the principal cusp, are 3 additional cusps, as well as 2 in the following front-to-rear row (Fig. 8B). Tooth XI, finally, which is the most complex, has 21 additional cusps: 6 each in the anterior and posterior rows, 1 external and 8 internal to the principal cusp. Directly internal to the principal cusp are 6 additional cusps in 2 front-to-rear rows (Fig. 8A). The cusps in the middle transverse row are less well developed than those in the end rows, but the arrangement of the additional cusps by twos and threes in the middle row reveals a tendency toward differentiation.

It is interesting to note that Romer (1961), on the basis of the drawings accompanying Konzhukova's article (1949), concluded that in the upper "molars" of *"Permocynodon"* the principal cusp was located at the inner edge of the crown. Romer stated that on the basis of this one characteristic, *"Permocynodon"* could be set apart from all the other cynodonts. His interpretation of the arrangement of the upper "molars" is erroneous simply because he was not aware of the damage to the inner sides of the crowns of the teeth since it was not shown in Konzhukova's illustrations. He also supposed that in the lower "molars" of *"Permocynodon"* the principal cusp was accordingly located at the outer edge of the crown. It is ironic that Romer's interpretation of the structure of the lower "molars" in *"Permocynodon,"* which was based on inadequate illustrations of the upper molars, quite unexpectedly anticipated the true picture.

DENTAL SUCCESSION

The conditions of preservation and the lack of replacing teeth make it impossible to trace the dental succession in *Dvinia* with any high degree of precision. The succession pattern can be judged only from the sizes of the pits (alveoli) for the succeeding teeth, which are fairly distinct for the "premolars" in the fragment PIN 2245/237 and for the "molars" in the left branch of the lower jaw of the *"Permocynodon sushkini"* holotype (PIN 2005/2469). As in the typical South African theriodonts (*Thrinaxodon:* Parrington, 1936; Crompton, 1963b; Hopson, 1964a; *Bauria* and *Ericiolacerta:* Crompton, 1962), the dental succession was alternating, with separate succession waves in the even- and odd-numbered series. On the left side of *Dvinia's* lower jaw the following waves of replacement can be made out:

1. *Odd series.* The first series (from the rear) includes the replacing teeth XV and XIII and the functioning teeth XI, IX and (?) VII. The second succession series includes the replacing teeth XI, IX, VII and (?) V and the functioning teeth III and (?) I. The third series apparently includes the replacing teeth III and I.

2. *Even series.* The first even series (from the rear) includes the replacing teeth XIV, XII, X and (?) VIII and the functioning teeth VI, IV and (?) II. The second series includes the replacing teeth VI, IV and (?) II. In the upper jaw of the fragment PIN 2245/237 there are two odd series (the first: replacing teeth VII and V and functioning teeth III and I; second: replacing teeth III and I) and two even series (first: replacing teeth VI and IV and functioning tooth II; second: replacing tooth II). Thus there were up to 5 waves of succession at the same time in each jaw. The "premolars" and the "molars" are in the same series.

As in the gomphodont cynodonts of the *Diademodon* type (Fourie, 1963), however, postcanines I and II may, as the animal grew older, have been displaced by the canine, and posterior to them the tooth row may thus have been lengthened by the addition of new "molars." In the smallest of the Northern Dvina cynodonts (specimen PIN 2245/237) 12 postcanines are present in all, 6 of them "molars." In the intermediate-sized specimen PIN 2005/2469 (the *"Permocynodon sushkini"* holotype) there were also 12 functioning postcanines present, but the anterior "premolar" was evidently lost, and the number of "molars" increased

to 7. The largest specimen, the *D. prima* holotype PIN 2005/2465, has 13 functioning teeth, of which 7 are "molars."

The dental succession pattern characteristic of the Northern Dvina cynodonts seems at first glance to have been more primitive than that in the therocephalian *Moschowhaitsia* (Tatarinov, 1965a) and the dinocephalian *Estemmenosuchus* (Kalandadze, in press) in which both the even and the odd teeth succeed in the same wave. Yet the real difference between the two types of succession patterns is small. In comparison to the usual reptiles, in *Moscho-whaitsia* there is a somewhat greater interval between the succes-sive generations of new teeth (up to 3 tooth intervals instead of the usual 2.5) and the succession rate is a little slower. Both succession patterns are due to the passage of waves of succession along the jaw from rear to front, at definite intervals (Edmund, 1960).

EVOLUTION TOWARD A GRINDING DENTITION

The unique systematic position of *Dvinia* is determined in many respects by its adaptation to a specific way of life. Here we have a peculiar "attempt" to evolve a grinding dentition out of the former sectorial specialization of the teeth in the primitive theri-donts. As in the latter, the lower teeth of *Dvinia* lay inside the upper when the mouth was closed. But in mastication, the greatly widened "molars" of *Dvinia* pressed the fodder against hard skeletal platforms (the bony secondary palate and the horizontal shelf on the lower jaw) and cut up or ground the food against it. These bony platforms were quite likely covered by horny epithe-lium, as indicated by the roughness of their surfaces. The upper and lower "molars" were not functionally equivalent. The main role in grinding the fodder was evidently played by the lower "molars" with their wider and more complex crowns. The upper "molars," which have relatively well developed principal cusps, apparently aided in piercing or tearing the food.

This type of dentition for grinding food appears to have been less efficient than the usual form (with occluding upper and lower teeth), so that we can properly speak of non-adaptive specializa-tion of the *Dvinia* dentition. As in other typical cases of non-adap-tive specialization (Schmalhausen, 1946), we see in *Dvinia* a retention of the old correlative relationships (the type of occlusion

was inherited by *Dvinia* from the primitive theriodonts), combined with a rapid rate of specialization (*Dvinia* is unique among the upper Permian theriodonts in the complexity of its "molars"). *Dvinia's* unsatisfactory grinding dentition was compensated for, to some degree, by the great strengthening of the temporal muscle. Efficient use of this muscle was facilitated by the ventral displacement of the mandibular articulation. The movements of the lower jaw were confined to a single plane by the involvement of the quadratojugal and the surangular in the mandibular articulation.

It is difficult to draw definite conclusions about the nature of *Dvinia's* food. The retention of laterally compressed canines testifies against the thorough adaptation to an herbivorous diet which is suggested by the complex structure of the "molars." It is fully possible, however, that *Dvinia* lived on an omnivorous diet. This may have included large insects with hard carapaces, which would have been easily broken (crushed) by *Dvinia's* "molars." It is quite obvious that the grinding force was concentrated in *Dvinia's* posterior postcanines (the "molars"), which have very complex crowns adapted for grinding. The role of the anterior postcanines (the "premolars") in grinding the food was relatively small. The external differentiation of the postcanine teeth into "premolars" and "molars" is more strongly manifested in *Dvinia* than in cynodonts of the type of *Diademodon* (Brink, 1955). The further decrease in the grinding function of the "precanine" teeth in the Traversodontidae may have led to the formation of a distinct diastem between the canines and the cheek teeth (as in *Exaeretodon frenguellii* from the Middle Triassic deposits of South America; Bonaparte, 1963b).

ACKNOWLEDGEMENTS

ABBREVIATIONS

ac — anterior canine
al — position of the lateral mandibular articulation
An — angular
apa — articular facet of the proatlas
Ar — articular
ats — foramen for a. temporalis superficialis (?)
Bo — basioccipital
Bs — basisphenoid
C — coronoid process
Ca — precoronoid
cc — carotid canal
cf — floccular canal
co — occipital condyle
cra — angular crista
cv — vidian canal
D — dentary
dl — lacrimal duct
Ec — ectopterygoid
Eo — exoccipital
Ep — epipterygoid
F — frontal
fa — adductores fossa
fc — condyloid foramen
fch — foramen for chorda tympani nerve
fci — fossa for lower canine
fcso — posterior ventral foramen of the suborbital canal
fcsod — posterior dorsal foramen of the suborbital canal
fh — hyoid fossa (?)
fi — foramen incisivum
fip — palatine fissure
fj — jugular foramen
fm — mental foramen
fmp — posterior mental foramen
fmx — maxillary fossa
fo — fenestra ovalis
fp — major palatine foramen
fpp — pterygo-paroccipital foramen
fpt — posttemporal foramen

fq — quadrate foramen
fqa — additional quadrate foramen
fr — fenestra rotunda
fs — suborbital foramen
fsm — septomaxillary foramen
fst — stylomastoid foramen
fv — emissary foramen
fvo — vomerine fossa
hs — horizontal shelf of the dentale
ip — prootic incisure
ipt — interpterygoid vacuity
iv — emissary cleft
J — jugal
L — lacrimal
la — anterior lamina of the prootic
mae— external acoustic meatus
maep — insertion of the posterior pars of the external adductor
mdl — depressor labii inferioris
"mms" — hypothetical insertion of the superficial masseter
mst — muscle scar of M. stapedius
mt — insertion of M. temporalis
Mx — maxilla
N — nasal
np— palatine foramen
nt — tympanic canaliculus
P — parietal
Pa — prearticular
paq — quadrate process of the paroccipital
pas — processus ascendens of the quadratojugal
pbp — basipterygoid process
pc — coronoid process
Pe — periotic
Pf — prefrontal
pf — falciform process of the quadratojugal
Pl — palatine
Pm — premaxilla
pm — mastoid process
pmu — muscular process of the periotic
Po — postorbital
Pp — postparietal

ppo — paroccipital process
pq — quadrate process of the periotic
pr — retroarticular process
psm — "stylomastoid process" of squamosal
pst — opisthotic process for the stapes
Pt — pterygoid
pt — pterygoid process of the periotic
ptr — transverse process of the pterygoid
Qj — quadratojugal
Qu — quadrate
r — rudimentary anterior postcanine
ret — epitympanic recess
rl — reflected lamina of the angular
Sa — surangular
Sm — septomaxilla
So — supraoccipital
Sp — splenial
Sq — squamosal
St — stapes
sv — vidian sulcus
T — tabular
V — vomer
vo — impression veni occipitalis
VI, VII, IX, X, XII — foramina for abducens, facial, glosso-
    pharyngeal, vagus, and hypoglossal nerves

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